Growth responses to climate and drought at the southernmost European limit of Mediterranean *Pinus pinaster* forests

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A B S T R A C T

Climate warming and increasing aridity may negatively impact forest productivity across southern Europe. A better understanding of growth responses to climate and drought in southernmost populations could provide insight on the vulnerability of those forests to aridification. Here we investigate growth responses to climate and drought in nine *Pinus pinaster* (maritime pine) stands situated in Andalusia, southern Europe. The effect of climatic variables (temperatures and precipitation) and drought on radial growth was studied using dendrochronology along biogeographic and ecological gradients. We analyzed old native stands with non-tapped and resin-tapped trees mixed, showing their usefulness in dendroclimatic studies. Our results indicate a high plasticity in the growth responses of maritime pine to climate and drought, suggesting that site aridity modulated these responses. The positive growth responses to spring precipitation and the negative responses to summer drought were stronger in the more xeric inland sites than in wet coastal ones, in particular from the 1980s onwards. The characterization of tree species' responses to climate at the southern or dry limits in relation to site conditions allows improving conservation strategies in drought-prone forest ecosystems.

1. Introduction

Climate models for southwestern Europe predict a decrease in annual mean precipitation between −6 and −14% and an increase in temperature up to +6 °C for the late 21st century (IPCC, 2013). In this drought-prone Mediterranean region, tree populations forming the southernmost distribution limit of the species (usually regarded as the climatic margin of tolerance; cf. Sánchez-Salguero et al., 2012, 2017) are considered to be more sensitive to climate warming and related aridification trends (Hampe and Petit, 2005). Climate warming could lead to a decrease in forest productivity from increased drought stress so understanding the tree growth response to warmer and drier conditions is a key issue in forestry (Lindner et al., 2014). Moreover these forest ecosystems may serve as valuable model for assessing how sensitive are tree populations in response to diverse humid to arid conditions across latitudinal or altitudinal gradients (Macias et al., 2006; Camarero et al., 2013).

The Maritime pine (*Pinus pinaster* Ait.) is a dominant species in western Mediterranean forests, with its main distribution area encompassing the Iberian Peninsula and also western Italy, SW France, and the High Atlas and Tunisia in North Africa (Blanco et al., 1997). The

Maritime pine is the conifer that occupies the largest area in Spain (around 1,200,000 ha, MMA, 2002) and 600,000 ha are considered as native stands (Alía et al., 1996). This species shows a wide ecological range, being able to withstand cold winters and warm summers characterizing the continental climate in central Spain, but it also grows well in temperate zones of the Atlantic or Mediterranean Iberian coast (Alía et al., 1996). It is adapted to survive under regular or variable rainfall regimes, and it tolerates droughts in the semi-arid southeastern Spain (Blanco et al., 1997; Carrión et al., 2000). This species shows high responsiveness to changes in drought severity (Camarero et al., 2015). The native populations grow on a great variety of substrates, although it is more common on acidic, loose and sandy soils (Blanco et al., 1997). Even though *P. pinaster* forests have been traditionally used for resin and wood production (Calama et al., 2010), other main uses of the species are related to recreation and soil protection (Anaya-Romero et al., 2016).

Dendroecological studies on *P. pinaster* have been conducted in southwest France (Timbal, 2002), Italy (De Micco et al., 2007; Mazza et al., 2014) and Tunisia (El Khorchani et al., 2007). In the Iberian Peninsula the main studies have focused on western (Vieira et al., 2009; Rozas et al., 2011b) and central Spain (Bogino and Bravo 2008; Candel-

Pérez et al., 2012; Génova et al., 2014). Detailed studies have also been conducted on intra-annual fluctuations in wood density (De Micco et al., 2007; Bogino and Bravo 2009; Vieira et al., 2009; Rozas et al., 2011a; Campelo et al., 2013). However, studies considering site aridity along ample climatic gradients are lacking for the southernmost stands in Europe located in the Iberian Peninsula (but see Sánchez-Salguero et al., 2010), where the xeric limit of the species distribution occurs. The Iberian *P. pinaster* forests are well adapted to withstand severe summer droughts (Alía et al., 1997; Correia et al., 2008). These southern pine forests display a high level of diversity and they have been identified as one of the dispersal centre of the species after the last glaciation (Salvador et al., 2000).

To assess the vulnerability of Iberian *P. pinaster* forests in the southernmost region, we quantify the growth response of this species to past climate variability and drought stress. We use a dendrochronological dataset from nine sites located in Andalusia, southern Europe, considering climate variability among sites, particularly comparing coastal and inland forests. As previous dendroecological studies in other Iberian pine species (Martín-Benito et al., 2010; Pasho et al., 2011; Sánchez-Salguero et al., 2012; Camarero et al., 2013; Natalini et al., 2016), we analyzed the spatial and temporal variability of growth- drought relationships. Our specific aims were: (1) to assess growth variability in the southernmost *P. pinaster* forests in Europe, (2) to examine the geographical patterns of growth responses to climate and drought, and (3) to test if radial growth − climate relationships were stable during the second half of the 20th century. We hypothesized that coastal *P. pinaster* populations subjected to the Mediterranean sea influence and more humid conditions will be the least responsive to precipitation and drought stress, whereas inland stands from more xeric sites will be the most sensitive to water shortage and spring precipitation. To test these hypotheses, we examined radial growth − climate associations and their variability over space and time.

2. Material and methods

2.1. Study area

The study area is located in the Baetic mountain ranges, Andalusia, southeastern Spain (Fig. 1a). These mountain systems constitute the most extensive range of the Peninsula, which extends for ca. 600 km, from the Strait of Gibraltar to the Cape of the Nao with the highest peak of the Peninsula (Mulhacén, 3479 m a.s.l.). The Baetic mountain ranges lie on both sides of the Guadalquivir River Basin, with palaeozoic and siliceous materials dominant in the north, and limestone and sandstone substrates prevailing in the south. Native *P. pinaster* forests in Andalusia are dominant in south-oriented slopes and mid-elevation sites (600–1700 m a.s.l), and occupy ca. 200,000 ha (Fig. 1) (REDIAM, 2009). Regarding the provenance regions (Table 1), in the Sierra Segura-Alcaraz (the most inland region), *P. pinaster* lives between 600 and 1700 m a.s.l. on limestones and dolomites and may concur with *Pinus halepensis* Mill. (low-elevation) and *Pinus nigra* L. in high-elevation sites. In the Sierra Almijara-Nevada, more southerly area but still with influences of continental Mediterranean climate, it lives at higher elevation range (1000–1800 m a.s.l.) on similar substrates. Regarding precipitation, both regions have similar values, being higher when elevation increases. The Sierra Bermeja provenance region is the southernmost and are located more closer to the coast; *P. pinaster* lives at lower elevation (200–1400 m a.s.l.) on a very different substrate (peridotites) and may form mixed forests with Spanish fir (*Abies pinsapo* Boiss.) (Alía et al., 1996).

2.2. Climate data

The climate of the study area is Mediterranean. Monthly climatic data (mean, maximum and minimum temperatures and total precipitation) for the period 1950–2012 were used to characterize climatic

conditions. We selected this period because there are few meteorological stations located near the study sites providing reliable climate data prior to the 1950s (Brunet et al., 2006). The data were obtained from the Climate Research Unit (CRU TS 4.01, http://ww.cru.uea.ac.uk/es). This dataset corresponds to interpolated data of instrumental records recorded by a dense network of local meteorological stations, which have been subjected to homogeneity tests and relative adjustments, and finally gridded onto a 0.5° network (Harris and Jones, 2017). Temporal trends in the monthly temperature and seasonal precipitation were calculated to characterize the climate tendencies of the site (Table 1; Fig. 2).

To estimate the effect of drought intensity and duration on radial growth, we used the Standardized Precipitation–Evapotranspiration Index (SPEI), which is calculated using precipitation and temperature data from the same homogeneous and spatially dense dataset of local observatories than CRU climate data (Vicente-Serrano et al., 2010). The SPEI varies from negative to positive values corresponding to dry and wet periods, respectively. The SPEI monthly values were calculated for the studied sites considering the period 1950–2012 and 1–24-month-long scales since this is a multiscalar index. The SPEI accounts for the negative effect of warmer temperatures on water availability by statistically modelling cumulative water balances. Therefore, different SPEIs are obtained for different time scales representing the cumulative water balance over the previous months (Vicente-Serrano et al., 2010). The SPEI is useful to identify time-dependent growth response to drought scales (see Pasho et al., 2011).

2.3. Field sampling and dendrochronological methods

We selected nine sites encompassing different environments and provenances in which *P. pinaster* grows in the region (Fig. 1, and see sites' codes in Table 1). The sampled sites were distributed both in the northern inland Prebaetic mountain ranges (Cazorla and Las Villas in the Sierra Segura- Alcaraz provenance) and in the southern Penibaetic (Trevenque, Albuñuelas, Almijara and Cómpeta in the Sierra Almijara-Nevada provenance and Bermeja in the Sierra Bermeja provenance). The main types of substrates are representative of the region, limestones and dolomites in all most localities, except peridotites in the coastal site PIBE, and usually the soils are rocky and shallow. The average elevation is 1222 m a.s.l., reaching the maximum value in the PITR site (1780 m a.s.l.). The resin production has been significant throughout the region, including areas as Albuñuelas (PIAB site), Cazorla (PCA1 and PCA2 sites) and especially in Cómpeta and Almijara (PICO and PIAL sites), the latter site was indeed located close to the Factory "Unión Resinera Española", which ended its activity in 1975 (Araque Jiménez, 2012). However, resin production has abandoned in recent decades (García-Iruela et al., 2016).

At each site, we selected dominant trees separated by at least 10–20 m from each other, looking for the oldest *P. pinaster* and including both non-tapped (64% of sampled trees) as well as resin-tapped trees (36% of sampled trees). We also considered resin-tapped trees after previous studies revealed that there were no consistent differences in climatic responses between resin-tapped and non-tapped trees of *P. pinaster* and *P. sylvestris* (Génova et al., 2014; van der Maaten et al., 2017). We sampled a minimum of 13 trees per site up to a maximum of 55 trees and we measured dendrometric and other tree and site attributes (Table 2). Two to three cores per tree at 1.3 m height were collected with a Pressler increment borer along the perpendicular direction to maximum slope. The cores were air dried and cut in transverse section with a razor blade until tree-rings became clearly visible. Samples were visually cross-dated, and the tree-ring widths were measured to the nearest 0.01 mm using a LINTAB™ measuring device (Rinntech, Heidelberg, Germany). Cross-dating quality was checked using the program COFECHA (Holmes, 1983) by checking the consistency of the different ring width series among trees coexisting within the same site.
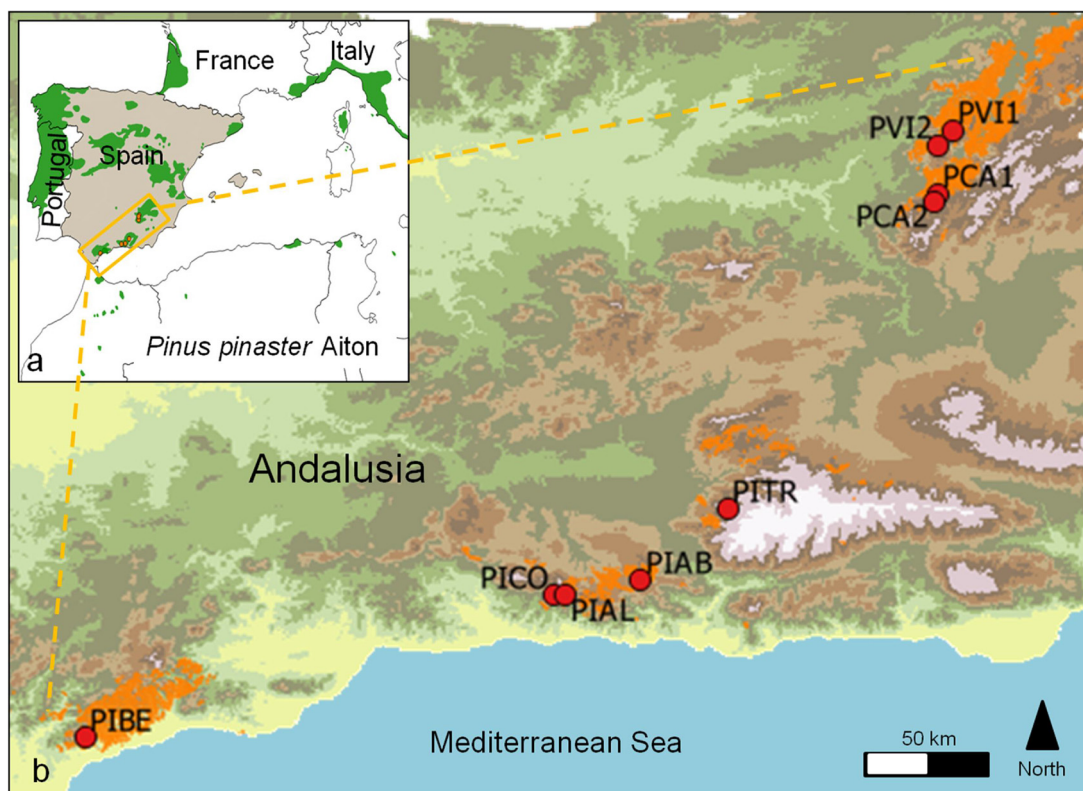
Fig. 1. (a) Southwestern distribution of *Pinus pinaster* and (b) sampled sites (red dots) in Andalusia (southern Spain) with *P. pinaster* distribution (orange patches) and digital elevation model in the background. Sites' codes are as in Table 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

To quantify radial growth − climate associations, tree-ring widths were converted into indices (TRWi) by standardizing and detrending raw data for each tree using the program ARSTAN v.44 (Cook, 1985). Each ring-width series was double-detrended, fitting a negative exponential function followed by a 30-year long spline to retain high-frequency variability. Detrending allowed transforming tree-ring widths to dimensionless growth indexes by dividing observed ring width values by fitted values. The resulting series were pre-whitened by autoregressive models to remove temporal autocorrelation. Lastly, a biweight robust mean was computed to obtain a residual chronology for each site which was used in all subsequent analyses.

To assess the quality of tree-ring width series several dendrochronological statistics were calculated considering the common period 1950–2012 (Fritts, 2001): first-order autocorrelation of raw width data (AC), mean sensitivity (MS) of indexed growth values, mean correlation between trees (rbt), variance accounted for by the first principal component (PC1) and the Expressed Population Signal (EPS),

which measures the statistical quality of the mean site chronology compared with a perfect infinitely replicated chronology (Wigley et al., 1984) (Table 2).

2.4. Relationships between radial growth, climate and drought

We quantified radial growth – climate associations using monthly and seasonal climate data. Climate data and chronologies of ring-width indices were related by calculating bootstrapped Pearson correlation coefficients for the common period 1950–2012. These correlations were calculated from previous August to current October, i.e., prior and during the year of tree-ring formation, based on previous analyses of Iberian *P. pinaster* growth responses to climate (Génova et al., 2014). To assess whether these relationships were stable through time, we calculated 20-year long moving correlations overlapping by one year, taking into consideration only those climate variables strongly and significantly ($P < 0.05$) correlated with TRWi. On the other hand, we

Table 1
Stands characteristics of the *Pinus pinaster* forests sampled in Andalusia, southern Spain. Sites are ordered from North to South.

Provenance[*]	Site name	Code	Latitude (°N)	Longitude (°W)	Average Elevation (m a.s.l.)	Substrate[†]	Aspect	Slope (°)	Mean annual temperature (°C)	Total annual Precipitation (mm)
Sierra de Alcaraz,	Las Villas I	PVI1	38.10	2.88	1050	L/D	S	31	13.6	445
Cazorla, Segura y las	Las Villas II	PVI2	38.06	2.92	1350	L/D	S	10	12.7	559
Villas	Cazorla I	PCA1	37.93	2.92	970	L/D	NW	22	14.4	448
	Cazorla II	PCA2	37.91	2.93	1400	L/D	W	33	13.5	568
Sierra de Tejeda-	Trevenque	PITR	37.09	3.48	1780	D	SW	20	11.8	530
Almijara, Alhama y	Albuñuelas	PIAB	36.90	3.71	1200	L	SW	28	15.8	450
Nevada	Almijara	PIAL	36.86	3.91	1380	D	S	35	15.5	454
	Cómpeta	PICO	36.86	3.94	1110	D	S	20	16.0	448
Sierra Bermeja	Bermeja	PIBE	36.48	5.19	900	P	NE	12	17.6	627

[*] See Alía et al. (1996).
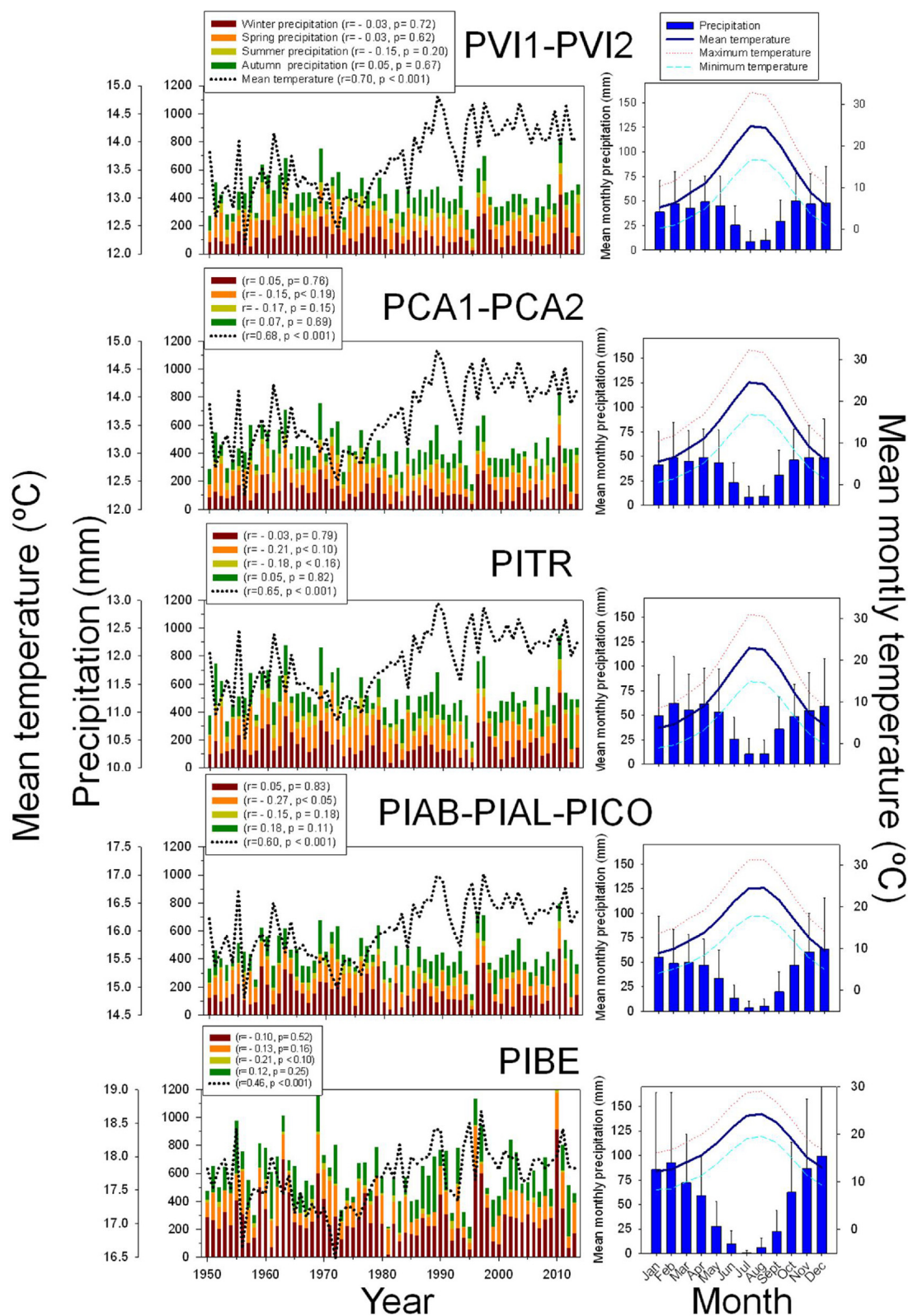[†] Abbreviations: L, limestones; D, dolomites; P, peridotites.

Fig. 2. Climatic trends (Pearson correlation coefficients; *r*) in mean temperature (lines) and seasonal precipitation (bars, left column), and climatic diagrams (right column) of the studied sites (see Table 1 for sites' codes) for the period 1950–2012 based on the CRU TS 4.01 climate dataset ((Harris and Jones, 2017). The statistics show the corresponding significance levels (*P*).

Table 2
Size, mean age, growth variables and related dendrochronological statistics based on radial-growth series for each studied sites. The statistics and mean ring-width values (SD stands out for standard deviation) were calculated for the common period 1950–2012. All dendrochronological statistics were calculated for residual chronologies excepting AC which was obtained for raw tree-ring width data.

Site code	No trees	DBH ± SD (cm)	Age ± SD (years)	Ring-width, mean ± SD (mm)	AC*	rbt	MS	Time span (years)	PC1 (%)	EPS (1950–2012)
PVI1	18	68.3 ± 4.9	134 ± 37	1.26 ± 0.72	0.871	0.490	0.241	1813–2012	40.53	0.953
PVI2	13	73.7 ± 4.4	193 ± 31	0.98 ± 0.31	0.867	0.577	0.224	1783–2012	43.26	0.934
PCA1	19	82.7 ± 27.6	164 ± 22	0.95 ± 0.46	0.910	0.594	0.237	1794–2012	54.10	0.902
PCA2	40	75.4 ± 10.1	115 ± 25	1.35 ± 0.68	0.911	0.660	0.232	1839–2012	54.72	0.982
PITR	30	71.6 ± 11.3	123 ± 13	1.22 ± 0.59	0.821	0.627	0.272	1873–2013	54.05	0.954
PIAB	55	64.9 ± 10.5	135 ± 26	0.82 ± 0.95	0.931	0.613	0.224	1825–2013	39.76	0.984
PIAL	15	51.2 ± 4.4	172 ± 44	0.72 ± 0.37	0.857	0.485	0.231	1751–2012	47.28	0.933
PICO	19	63.0 ± 9.7	140 ± 33	1.29 ± 0.89	0.822	0.586	0.256	1833–2012	39.36	0.924
PIBE	31	54.4 ± 4.9	148 ± 37	0.77 ± 0.52	0.902	0.561	0.213	1777–2012	45.98	0.972

*Abbreviations: AC, first-order autocorrelation; *rbt*, mean between-trees correlation of ring-width indices; MS, mean sensitivity; PC1, variance accounted for by the first principal component; EPS, Expressed Population Signal (Wigley et al., 1984).
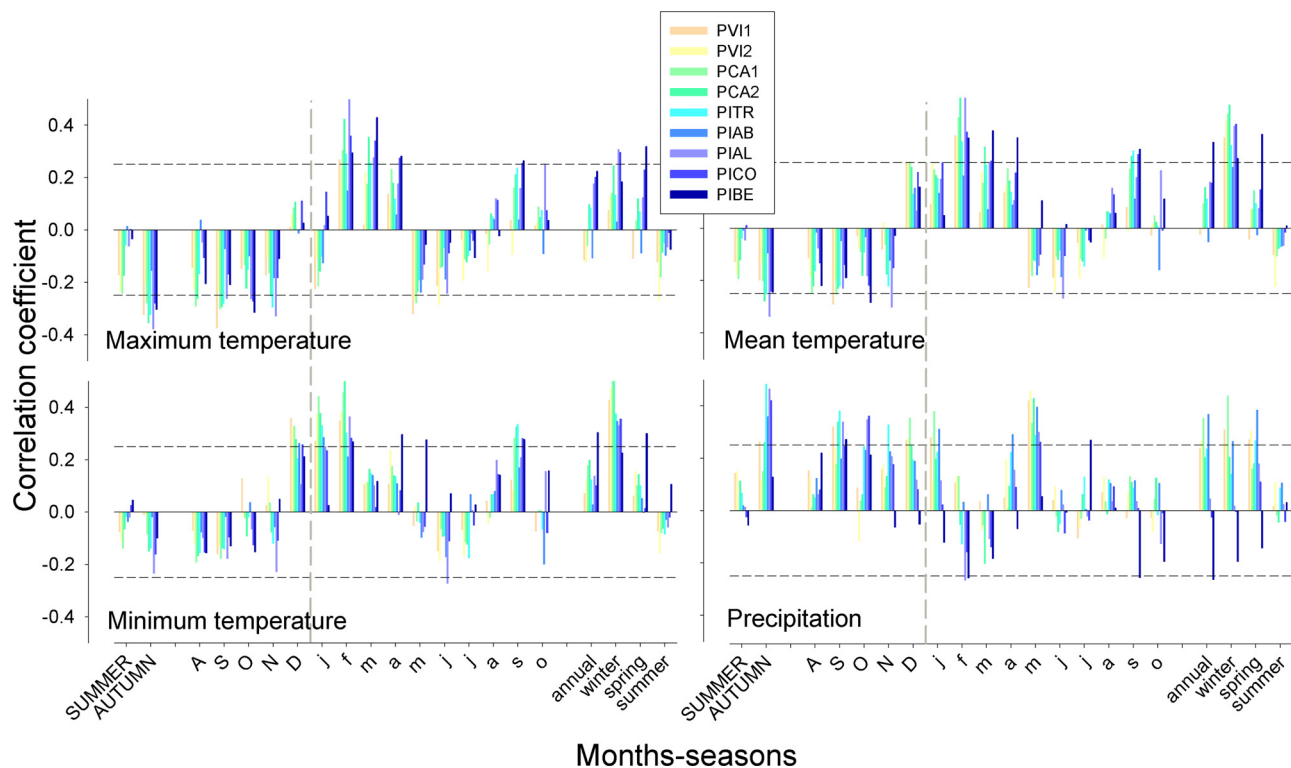
Fig. 3. Bootstrapped tree growth-climate associations for the studied sites assessed by relating ring-width indices (TRWi) to seasonal and monthly climatic variables (maximum, minimum, mean temperature and precipitation). The temporal window of analyses includes from previous August (previous-year months and seasons are abbreviated by uppercase letters) up to current October (current-year months and seasons are abbreviated by lowercase letters). Significance levels are shown with dashed (*P* < .05) lines. Sites' codes are as in Table 1.

also calculated correlations between TRWi and SPEI obtained for 1- to 24-month long scales (Pasho et al., 2011). Bootstrapped and moving correlations were calculated using the software Dendroclim2002 (Biondi and Waikul, 2004).

3. Results

3.1. Chronologies characteristics

The sampled *P. pinaster* stands were on average 147 years old and to our knowledge are the longest chronologies elaborated with this species. The mean ring-width values for the common period 1950–2012 ranged from 0.72 to 1.35 mm, varying mainly in accordance with the mean age (Table 2). The correlation of growth series among trees (*rbt*) within each stand varied from 0.485 (PIAL) to 0.660 (PCA2) (Table 2), confirming a high growth coherency among trees from the same site.

Moreover, correlations among site TRWi series were high and coherent within the provenance regions, varying from 0.73 and 0.53, indicating a common response to regional climatic trends. There was also high correlation according to elevation; sites located at higher elevation (PV2, PC2 and PITR) showed correlations between their TRWi series which ranged 0.76–0.54, and correlations between sites located at lower elevation (PV1, PC1, PIAL, PIAB and PICO) ranged from 0.77 to 0.34. The lowest correlations corresponded to Sierra Bermeja provenance (PIBE site) and the other sites, and they ranged from 0.62 to 0.29.

3.2. Climate trends and radial growth – climate associations

The climatic diagrams (Fig. 2) represented the typical Mediterranean climate with summer aridity (especially from June to August), but in which differences are noted between the sites. The average temperature increased from the northern (PV1, 13.6 °C) to the
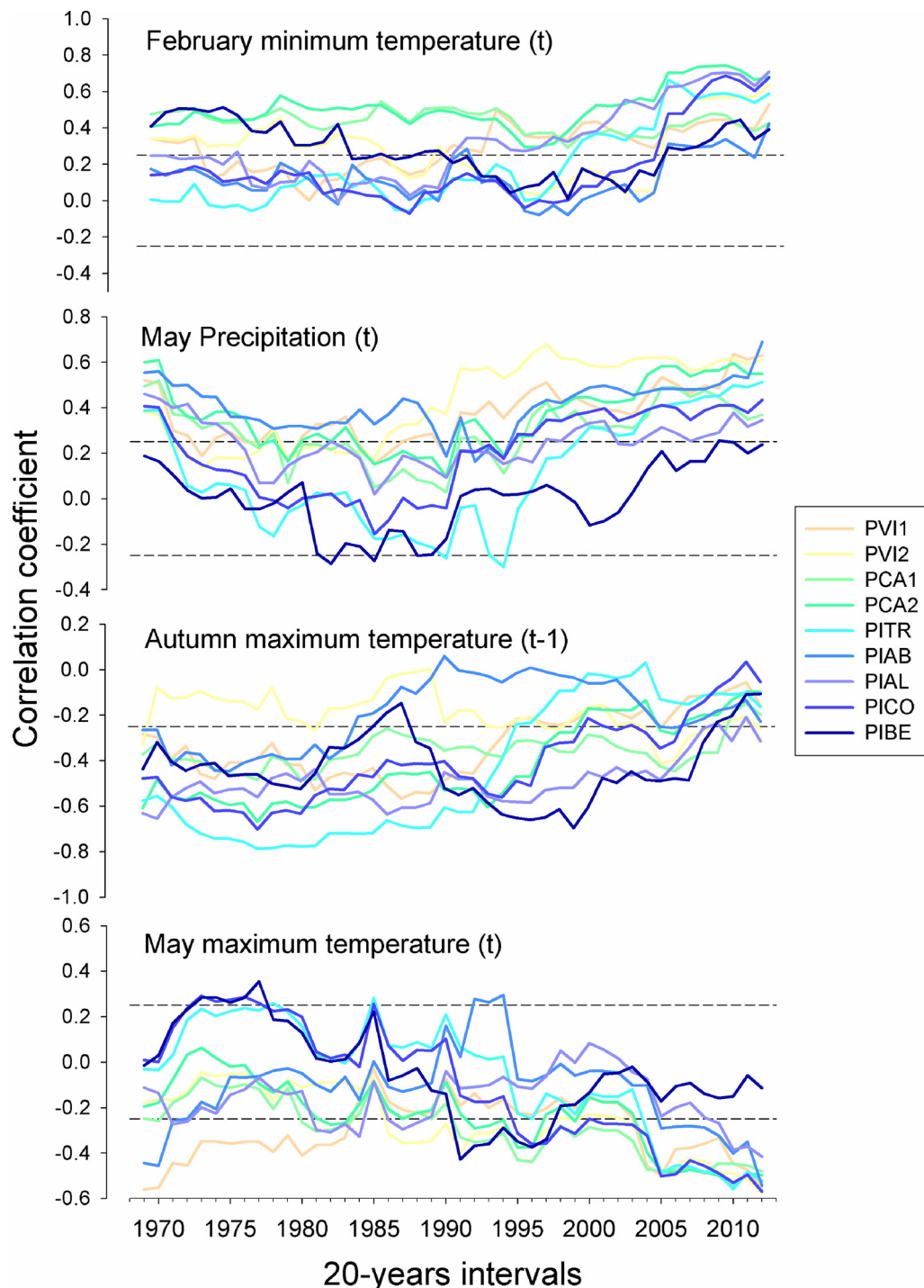
Fig. 4. Temporal changes in bootstrapped correlation coefficients using 20-year long intervals shifted by one year for the period 1950–2012 (values are arranged for the last year of each 20-year long interval). Dashed horizontal lines indicate statistically significant correlation coefficients (*P* < .05) for current (year t) February minimum temperature, current May precipitation, previous (year t-1) autumn maximum temperature and current May maximum temperature. Sites' codes are as in Table 1.

southernmost sites (PIBE, 17.6 °C), although in high-elevation sites (PITR, 1780 m a.s.l.) it can be less than 12 °C. Regarding the annual rainfall, the average values varied 445–454 mm in the driest sites (PV1, PC1, PIAL, PIAB and PICO), 530–568 mm in mesic sites, located at higher altitude (PV2, PC2 and PITR), and up to more than 600 mm in the southernmost and lowest altitude site (PIBE, the wettest site) (Table 1). This site is the only one located at the northeast-facing slope (Table 1). In the study area we found significantly (P < .001) rising trends in temperatures since 1950, particularly after the 1970s (Fig. 2). Temperatures increased at average rates from +0.01° to

+0.05 °C yr^{-1}. However, there were no trends regarding precipitation.

Tree growth in the nine stands was enhanced by higher winter temperatures, particularly minimum and maximum February temperatures, but it was limited by the previous autumn maximum temperatures (Fig. 3). Regarding the influence of precipitation we observed differences according to the provenance regions: in the Sierra Segura-Alcaraz (PCAs, PVIs) wet winter (January) and wet spring (May) enhanced higher *P. pinaster* growth, whereas wet previous autumn promoted it particularly in Sierra Almijara-Nevada provenance (Fig. 3). On the other hand, in the most humid site (Sierra Bermeja provenance,
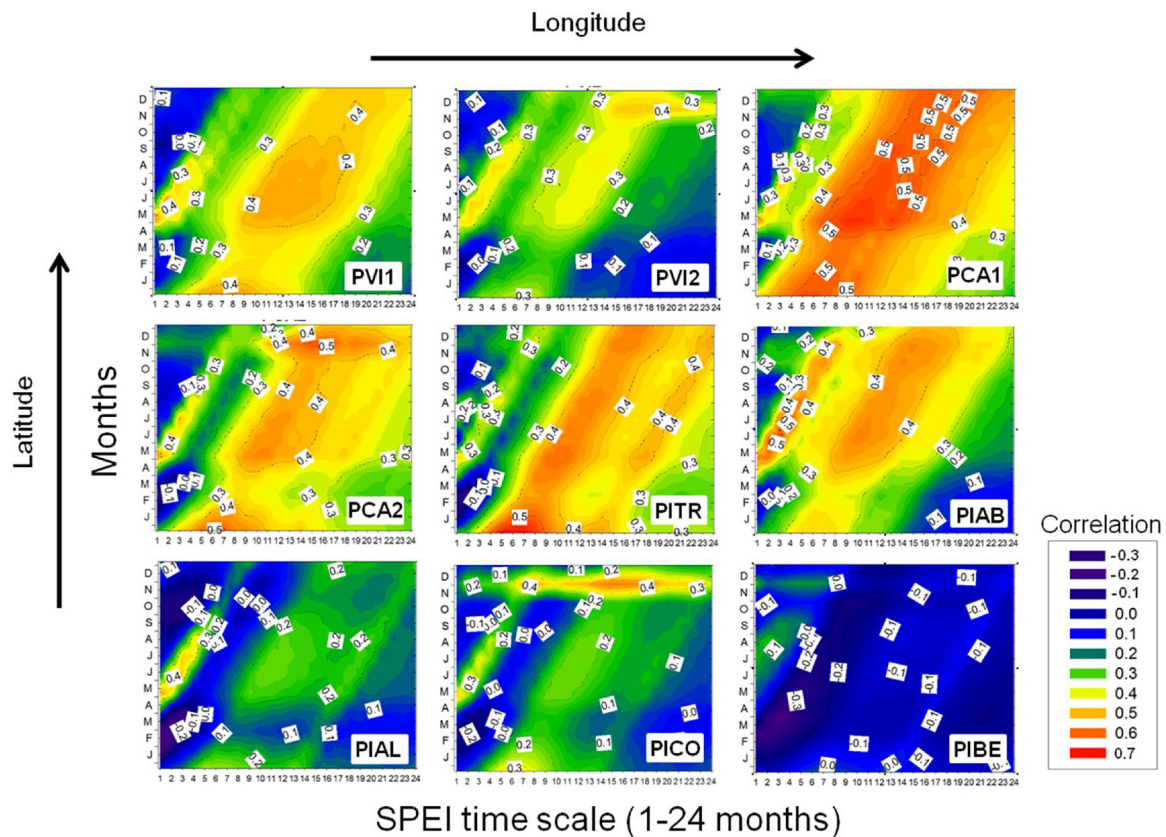
Fig. 5. Drought-growth associations of the studied sites ordered by latitude and longitude (from the left to the right for respective rows) assessed by relating ring-width indices (TRWi) to the Standardized Precipitation–Evapotranspiration Index (SPEI) considering up to 24-month long scales (*x* axes). Correlations were calculated for the common and best-replicated period 1950–2012 and considering the months of the current growth year (*y* axes). Correlation values above + 0.20 and below − 0.20 are significant at the *P* < .05 level. Sites' codes are as in Table 1.

PIBE), the tree growth- climate association was rather different that in the others sites: temperatures of spring and precipitation of July (positive association) and previous October temperature and February and September precipitation (negative association) were correlated with TRWi (Fig. 3).

Moving correlations between radial growth and the significant climate variables showed a noticeable shift in the 1980s with changes from negative to positive values and vice versa. The stronger influence of February minimum temperature increased in all sites, particularly in the Sierra Almijara-Nevada provenance and especially at higher elevation (i.e., PITR, the coldest site; Fig. 4). In the same way, the relationships with precipitation and maximum temperatures of May had also increased, in positive and negative relation respectively, in almost all sites, but less in the wettest site PIBE. Whereas, on the contrary, the correlation with the previous autumn temperatures changed from negative to no significant values (Fig. 4).

### 3.3. Associations between radial growth and drought

The correlations analysis between TRWi and SPEI showed a significant association between growth and intensity and severity drought increasing with latitude and decreasing with longitude, i.e., as we moved from the coast to inland (Figs. 1 and 5). We found a positive and significant relationship between SPEI recorded at 1–12 month long scales in all sites (except PIBE), corresponding to short dry or wet periods occurring at a high frequency (Figs. 5 and 6). In the Sierra Segura-Alcaraz provenance (the most inland sites, i.e., PVIs and PCAs) significant SPEI-growth correlations were found for time scales varying from 1 to 18 months and up to 24 months long, lower in the higher elevation sites (PVI2, PCA2; Fig. 5). In the Sierra Almijara-Nevada

provenance differences were observed from the inland sites (PITR, PIAB) with higher correlations, than the coastal ones (PIAL, PICO). The weakest drought-growth associations were determined at the Sierra Bermeja provenance (the wettest coastal site PIBE), where the associations between growth and SPEI were low or presented negative values, especially in late winter and early spring (Fig. 5). Finally, we observed similar high-frequency growth patterns (TRWi) as compared with those of the drought SPEI index (Fig. 6) with growth reductions (i.e., 1976, 1995, 2005) and growth increases (i.e., 1966, 1997). All the studied sites (except PIBE) showed significant correlations of TRWi with the SPEI drought index, representing high coherence between growth, drought severity and water availability.

4. Discussion

4.1. Radial growth – climate relationships

First, a positive effect of warmer winter (February) conditions on growth was detected, noted likewise for maritime pine in the center of Spain and central coast of Portugal (Génova et al., 2014; Campelo et al., 2013; Kurz-Besson et al., 2016). This may be due to an increasing earlier start of the cambial activity in relation to the increasing temperature determined for the last decades, as has been also postulated for other southern Mediterranean pine (Camarero et al., 2013). Second, lower spring precipitation (May) triggered negative effects on growth, as was also observed for *P. pinaster* in central, northwestern and eastern Spain (Bogino and Bravo, 2008; Rozas et al., 2011b, Candel-Pérez et al., 2012, Camarero et al., 2015), Portugal (Vieira et al., 2009, Kurz-Besson et al., 2016) and Sardinia, Italy (Mazza et al., 2014), suggesting that the radial growth is limited by water deficit during the growing season.
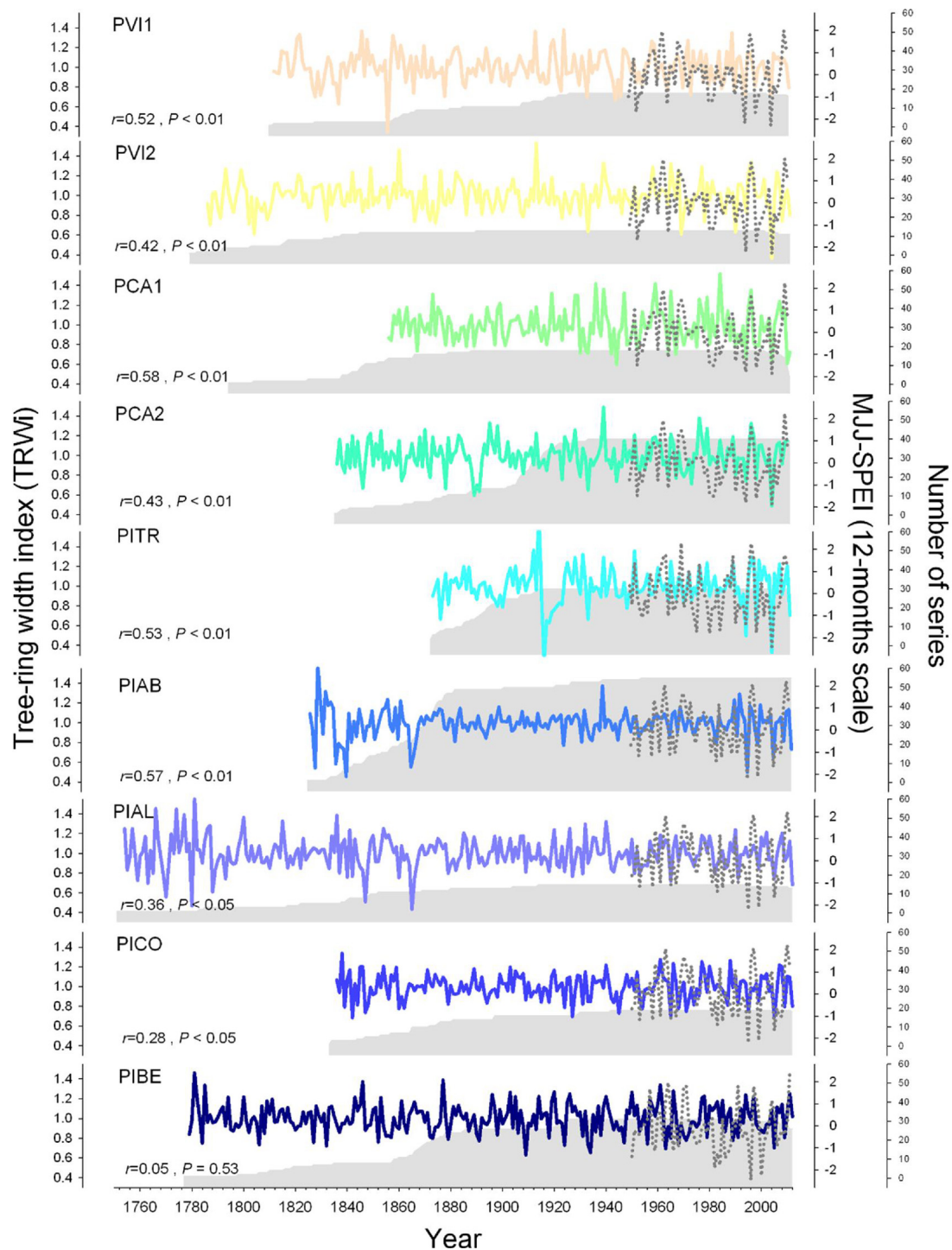
Fig. 6. Site chronologies (tree-ring width indices, TRWi; continuous lines) obtained for the studied stands and May to July Standardized Precipitation–Evapotranspiration Index (MJJ–SPEI) drought index calculated at 12-months long scales (dotted lines) for the 1950–2012 period. The plotted drought index was the most strongly related to the tree-ring width indices (TRWi) in most study sites (see Fig. 5). Pearson correlations (*r*) between TRWi and the MMJ–SPEI and associated probability values (*P*) are show for each site. Grey areas show the number of measured series for each site. Sites' codes are as in Table 1.

Finally, high temperatures along with low amounts of rainfall in the previous autumn negatively influenced maritime pine growth of the following year, which has also reported in central and northwestern Spain (Bogino and Bravo, 2008; Rozas et al., 2011b; Génova et al., 2014). According to Fritts (2001) and Andreu et al. (2007), warm late summers and autumns can prolong the growing season, limiting the formation of metabolic reserves and consequently reducing the amount of available carbohydrate resources for the following year. Otherwise, positive relationships of growth with high precipitations in previous autumn and winter could be related to a recharge of soil water reserves before the growing season enhancing the synthesis and mobilization of carbohydrates (Pasho et al., 2011). Reloading soil water before spring growth resumption is critical for Mediterranean conifer species inhabiting drought-prone areas with short springs and shallow or rocky soils such as the study sites. Such lagged radial growth − climate relationships agree with was has been found in other pine species from Mediterranean (Linares and Tíscar, 2010; Martín-Benito et al., 2010; Génova and Moya, 2012; Camarero et al., 2013; Sánchez-Salguero

et al., 2013) but also from dry subalpine sites (Oberhuber et al., 2015).

4.2. Temporal variability in radial growth – climate associations

The associations between radial growth and climate are strengthening during the last decades, with a noticeable shift which started in the 1980s. This is related to the increase of temperatures and drought in the studied area, particularly in spring and autumn (Fig. 2). During the second half of the 20th century an aridification trend affected most southern Spain and the recurrence of severe droughts caused a progressive reduction in available soil water (Ruiz Sinoga et al., 2011; Camarero et al., 2013; nchez-Salguero et al., 2012, 2013;). Therefore, a longer drought period might explain why *P. pinaster* radial growth – climate relationships shifted in the mid-1980s. Increasing drought stress during the second half of the 20th century might also be cause of the strengthening in the synchrony of tree growth (cf. Shestakova et al., 2016).

4.3. Tree growth responses to precipitation and drought are contingent on site aridity

There existed a relevant site-to-site variability modulating tree growth- climate responses. The radial growth in the most inland and xeric sites (Sierra Segura-Alcaraz provenance, PVIs and PCAs sites) showed a high sensitivity to growing-season precipitation, whereas growth in the coastal and humid PIBE site responded more to warm conditions in early spring. Moreover, we also observed that previous autumn conditions were more important for growth in the Sierra Almijara-Nevada provenance (PITR, PIAB, PIAL, PICO).

Regardless the magnitude of the growth-SPEI association and the time scale considered, the highest correlation coefficients between growth and the SPEI drought index were obtained in current spring and summer (May to July), the period when water balance is most negative. This positive relationships were higher in the stands with the highest water deficit (i.e., PCA1, $r = 0.58$, $P < .01$), being the driest and mesic sites of Sierra Segura-Alcaraz and the inland sites of Sierra Almijara-Nevada provenances those showing stronger growth responses to long-term (1–18 months) droughts. Trees growing in these sites responded to the SPEI drought index at long time scales, which indicates that cumulative precipitation conditions impact tree growth, as has been observed for *Pinus brutia* in the eastern Mediterranean (Sarris et al., 2007). On the other side, the wettest PIBE site showed no response to SPEI. It should be noted that the unusual PIBE location at northeast-facing slopes surely favors its water balance, especially during the dry summer. In the same way, the correlation analysis between TRWi and SPEI in the southern sites of the Sierra Segura- Alcaraz provenance (PIAL, PICO) are weaker comparing to the most inland sites (PITR, PIAB).

According to Chambel et al. (2007), *P. pinaster* shows a high divergence among populations in its responses to drought and drought could differently affect the maritime pine populations depending on local water availability and site aridity, as has been also observed in *P. nigra* (Martín-Benito et al., 2010; Camarero et al., 2013). The maritime pine could be locally adapted through morphological (e.g., deep roots) and physiological (e.g., tight stomatal regulation of water loss) features related with climate differences. Among these climate differences the coastal influence is important because in PIBE (the wettest site), but also in the drier PIAL and PICO sites, all of them located near the Mediterranean coast, the summer drought is likely alleviated by convective storms and coastal humid winds.

The characterization of tree species' responses to climate at the southern or dry limits in relation to site conditions allows improving conservation strategies in drought-prone forest ecosystems. Our results suggest that climate change might cause divergent growth trends in different *P. pinaster* populations (Fig. 6), as a function of drought stress modulated by biogeographical location, and highlight the site's

variability to take in account in further management and conservation programs.

5. Conclusions

The main climatic drivers affecting *P. pinaster* radial growth in its southernmost European distribution limit have been identified. The results highlighted the influence of local aridity conditions modulating the growth responses to climate, being the possitive influence of previous autumn rainfall on radial growth very relevant. Dry conditions during late spring constituted the major constraint of growth in xeric inland populations, which experienced more prolonged water shortage during the growing season than wet coastal ones. The radial growth responses to climate have increased and changed over time with a shift in the 1980s as climate warmed. Climate warming might cause divergent growth responses in different *P. pinaster* populations as a function of drought stress, site location and coastal influence.

Conflict of interest

The authors declare no conflict of interest.

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